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THE ABUNDANCE OF PREMETAMORPHIC NEWTS (*TRITURUS CRISTATUS*, *T. MARMORATUS*) AS A FUNCTION OF HABITAT DETERMINANTS: AN *A PRIORI* MODEL SELECTION APPROACH

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Despite the key role of premetamorphic amphibians in experimental ecology, the factors affecting their abundance has received relatively little attention in natural settings. We applied a model selection approach with AIC (Akaike's Information Criterion) to predict the abundance of embryos and larvae of crested and marbled newts (*Triturus cristatus* and *T. marmoratus*) at 32 breeding sites in western France, based on 15 variables describing the aquatic habitat, and 10 variables describing the terrestrial habitat within a 100 m radius around the pond. The best model for embryos included the variables shade and floating vegetation (highest embryo abundance in intermediate ponds), and pond size (negative correlation). Larval abundance was best explained by shade (negative correlation), and the interaction between phosphate and nitrate. Pond variables were not fully comparable to terrestrial parameters, but produced better predictive models for both embryos and larvae. Due to the high explanatory value of ecological parameters the results suggest that in a metapopulation context, deterministic population processes driven by pond succession may be more important than stochastic extinctions and recolonizations of otherwise suitable habitat patches.

Key words: AIC, ecological determinants, habitat selection, Urodela

INTRODUCTION

Understanding the factors that govern the distribution and abundance of species is a major goal of ecological research (Andrewartha & Birch, 1954). The distribution of pond-breeding amphibians is likely to be influenced by features of both the aquatic and the surrounding terrestrial habitat (Semlitsch, 2000, 2002). This is likely because populations of pond-breeding amphibians with aquatic eggs and larvae – and primarily terrestrial adults – can be regulated in the aquatic larval, terrestrial juvenile and terrestrial adult stage (Wilbur, 1980; Hellriegel, 2000; but see Biek *et al*., 2002). Even though the ecology of aquatic larvae has a long and successful history of experimental research (Smith, 1983; Wilbur, 1987, 1997), only a handful of studies has addressed the factors that affect their distribution and abundance in the field (e.g., Azevedo-Ramos & Magnusson, 1999; Gascon, 1991; Snodgrass *et al.*, 2000). In contrast, the ecological determinants that affect the distribution and abundance of adults have been documented intensively in descriptive studies (e.g., Skelly *et al.*, 1999; Pope *et al*., 2000; Joly *et al.*, 2001). To our knowledge no studies so far simultaneously examined the factors that may affect the abundance of the aquatic juvenile and the terrestrial adult stage.

As a part of our long-term research program on the ecological and evolutionary interactions among *Triturus* newts – primarily between *T. cristatus* and *T. marmoratus* and their hybrids (e.g. Arntzen & Hedlund, 1990; Arntzen & Wallis, 1991; Jehle & Arntzen, 2000) – we studied the environmental factors that may govern the abundance of these species in both the aquatic larval and terrestrial adult stages. Newts of the genus *Triturus* have a prolonged breeding period during which females usually wrap their eggs singly into leaves of aquatic vegetation (several hundreds per year). A full range of life stages (embryos, larvae, and adults) may hence be present in a pond at one time, with subadults and adults spending the majority of the year on land (Bell & Lawton, 1975; Griffiths, 1996). In the present paper we focused on determinants of the abundance of eggs and larvae. The abundance of eggs should largely reflect the adult population size (either the number of adults or their fecundity; embryo abundance *per se* is unlikely to affect adult abundance; Vonesh & De la Cruz, 2002), and we therefore assumed that embryo abundance is determined by features of the pond and the surrounding landscape, whereas the abundance of larvae should be affected by the presence of embryos and pond-specific factors that affect their growth and survival.

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TABLE 1. Environmental variables recorded for 32 study ponds in the Département Mayenne, western France.

Variable	Code	Specifier
AQUATIC		
Average slope of bank	BANK	<20, 21-40, 41-60, 61-80, >80% (1-5)
Decomposing leaves	LEAV	Absent, present (0,1)
Maximum pond depth	DEPTH	cm
Pond size	SIZE	m^2
Shade (canopy cover)	SHADE	0.1-20, 21-40, 41-60, >60% (1-4)
Turbidity of water	TURBID	Transparent, clear, moderate, opaque (1-4)
Floating vegetation	FLVEG	0-10, 11-20, 21-50, >50% (1-4)
Macrofauna	FAUNA	Sparse, moderate, abundant (1-3)
Marginal vegetation	MAVEG	0-10, 11-20, 21-50, >50% (1-4)
Submerged vegetation	SUVEG	0-10, 11-20, 21-50, >50% (1-4)
Predators	PRED	Sparse, moderate, abundant (1-3)
Nitrate (NO_3)	NIT	1, 3, 10, 30, 100 mg/l
Oxygen saturation	OXY	<30, 30-90, >90% (1-3)
pH	PH	
Phosphate (PO_4)	PHO	0.1, 0.2, 0.5, 1.0, 5.0 mg/l
TERRESTRIAL (100 M RANGE)		
Ditch	DITCH	Absent, present (0,1)
Arable fields	ARAB	Absent, present (0,1)
Hedges	HEDGE	Absent, present (0,1)
Marsh	MARSH	Absent, present (0,1)
Pasture	PAST	Absent, present (0,1)
Ponds	POND	Absent, present (0,1)
Relief	RELI	Flat, sloping, undulating (1-3)
Roads	ROAD	Absent, present (0,1)
Scrubs	SCRU	Absent, present (0,1)
Woodland	WOOD	Absent, present (0,1)

There is a large body of experimental and observational research on determinants of growth, survival, abundance, and distribution of amphibians. We used this knowledge to formulate hypotheses that reflected the results of these studies and our knowledge from many years of field work, and used information-theoretic model selection tools to assess whether these *a priori* hypotheses were supported by the data that we collected (Burnham & Anderson, 1998). Our analysis was therefore primarily confirmatory and did not suffer from the well known problems that are inherent in the exploratory and null hypothesis-based analysis of large observational data sets (Johnson, 1999; Burnham & Anderson, 1998; Anderson *et al*., 2000; Olden & Jackson, 2000; Anderson *et al*., 2001).

METHODS

STUDY AREA

Thirty-two ponds were studied, located in an area of ca. 12 × 33 km in the Département Mayenne, western France. Hilly and wooded areas in the north of the Département are occupied mostly by *T. marmoratus*, whereas flat and open areas in the south are occupied mostly by *T. cristatus*. The central study area is intermediate in its characteristics, including both terrestrial habitat types, and breeding ponds are regularly shared by both species. The landscape is gently undulating, comprising pasture for cattle breeding, with a relatively high density of hedgerows and small woodlands. Most ponds are man made. For a more detailed description of the study ponds and study area see Schoorl & Zuiderwijk (1981) and Arntzen & Wallis (1991).

ENVIRONMENTAL DATA

For each site, we collected 15 habitat variables characteriszing the pond and 10 variables characterizing the terrestrial habitat within a 100 m radius (Table 1; scored as in Scribner *et al*., 2001), encompassing 95% of terrestrial refuges of radio-tracked individuals (Jehle, 2000). Oxygen saturation was measured with a WTW Microprocessor Oximeter OXI 196 at a depth of 20 cm. As daily fluctuations reduced the power of single oxy-

TABLE 2. *A priori* models considered to relate the effects of aquatic and terrestrial habitat parameters to *Triturus cristatus* and *T. marmoratus* embryo abundance. (+) positive effects (-) negative effects; intercept refers to the value on the *y*-axis where the line defined by the regression equation crosses the axis (if the complete absence of predictor variables has meaning, then the intercept represents that amount).* This model includes the parameters best describing the abundance of larvae and it therefore stands for the hypothesis that embryo abundance and linked population size is influenced by the same parameters as larval abundance, and further that juvenile recruitment regulates population size and therefore number of eggs.

Model	Variables	Hypothesis	References
1	INTERCEPT	Random distribution	
2	POND	High abundance when number of adjacent ponds is small (–)	Scribner *et al.* (2001)
3	PRED	Newts avoid predator rich ponds (–)	Kats & Sih (1992)
4	SIZE, DEPTH	Large habitat patches support large populations (+)	Flather & Bevers (2002)
5	HEDGE, WOOD, ROAD	Important as terrestrial habitat, dispersal corridor (+), roads (–)	Findlay & Houlahan (1997), Jehle & Arntzen (2000), Joly *et al.* (2001)
6	FLVEG	Important as oviposition site (+)	Miaud (1995), Joly *et al.* (2001)
7	SHADE, SIZE, DEPTH	Canopy cover (–) and hydroperiod (+)	Skelly *et al.* (1999)
8	FLVEG, SIZE, HEDGE, SHADE	Aquatic and terrestrial habitat features are important, all (+) except Shade (–)	Joly *et al.* (2001), Miaud (1995), Skelly *et al.* (1999, 2002)
9	FLVEG, SIZE, SHADE	As 8, without hedge	
10 *	SHADE, NIT*PHO	Juvenile recruitment regulates population size, Shade (–), Nit*Pho (+)	Berven (1990)

gen measurements, ponds were classified by the maximum oxygen saturation reached in the early afternoon (13:00–15:00 hrs) on a sunny day, in the categories below 30%, from 30 to 90%, and 90% or above (1–3 respectively). Acidity was measured with an Amarell Electronic Pocket pH-Meter. Nitrate and phosphate concentration was measured with Dupla aquarium tests (1, 3, 10, 30 and 100 mg NO_3/l and 0.1, 0.2, 0.5, 1.0, and 5.0 mg PO_4/l). Environmental variables were recorded at the first visit at each pond from 30 April to 24 May 1999, during the main egg laying period. Water parameters were measured in the pond area where most eggs were detected. The abundance of predators (fish, dragonfly larvae, dytiscid beetles and their larvae) and macrofauna were recorded during dipnetting for larval newts between 20–29 June 1999. Abundance was classified according to the percentage of dipnet sweeps containing at least one individual as low (0–30%), moderate (31–60%), or high (>60%). All ecological and abundance data were collected by the same person (MS).

Abundance of *T. cristatus* and *T. marmoratus* Embryos and Larvae

We estimated the abundance of embryos by visual egg counts, classified into four size classes by the maximum number possible to obtain by one person in one hour, as low (<200 eggs), moderate (200<500 eggs), high (500<1000 eggs) or very high (>1000 eggs). All parts of each study pond containing vegetation appropriate as substrate for newt eggs were surveyed. Larval abundance was estimated by a standardized number of dipnet sweeps per pond, with 50, 100, 150 and 200 sweeps for small (<50 m^2), medium (<100 m^2), large (<300 m^2), and very large ponds (>300 m^2), respectively. Each dipnet sweeps was about 2.5 m wide, inserting the net at the most distant point and pulling it towards the body. All accessible sections of the pond were covered. We used the number of larvae per dipnet sweep as an index of the size of the larval population (Nichols, 1992; Anderson, 2001). The number of larvae per dipnet sweep was log (n + 1) transformed for statistical analysis (Zar, 1999). Embryos and small to medium-sized larvae of *T. cristatus* and *T. marmoratus* are not distinguishable in the field and occupy indiscernible spatial and habitat niches within ponds (Jehle *et al.*, 2000). Therefore, records for both species were pooled.

Model Selection

We used an information-theoretic model selection approach for the statistical analysis of the data (Burnham & Anderson, 1998; Anderson & Burnham, 2002). First, we used the published literature and our own knowledge from years of field work to build candidate statistical models that reflect biological hypotheses. The models are *a priori* because they were formulated before the data analysis. Tables 2 and 3 list the candidate models and state the biological hypoth-

eses, the factors included in the model, whether their effect was expected to be positive or negative, and the references from which the model was derived. To predict the abundance of embryos we chose models that included both aquatic and terrestrial variables. Models for larval abundance were set up using pond-related variables only and always included the variable "abundance of embryos" (EGG), as differences in embryo abundance between ponds would otherwise have made effects of ecological parameters undetectable. Given that the sample size was only 32, we (1) kept the number of models small; and (2) kept models simple, i.e. with a small to moderate number of factors and no interactions (except the nitrate by phosphate concentration interaction which reflects productivity) or quadratic terms. As a second step, we used the small-sample Akaike's Information Criterion AIC_c to rank models. AIC_c is defined as:

$$AIC_c = (\ln \mathcal{L}) + 2K + \frac{2K(K+1)}{n - K - 1}$$

where $(\ln \mathcal{L})$ is the natural logarithm of the likelihood function, K is the number of estimable parameters from that model, and n is the sample size (Burnham & Anderson, 1998). Model selection based on information theory does not require predictor variables to be uncorrelated (D. R. Anderson, pers. comm.). AIC_c estimates the support that a model receives from the data. The model with the lowest AIC value is the best supported by the data. The absolute value of AIC_c is not relevant; it is the difference in AIC_c between models i and the model with the lowest AIC_c value ($AIC_{c_{min}}$) ($\Delta AIC_{c_i} = AIC_{c_i} - AIC_{c_{min}}$) that gives information whether a model is relatively well or poorly supported. We also calculated the Akaike weights w_i for all models. Akaike weights are defined as:

$$w_i = \frac{\exp\left[-\left(\frac{\Delta AICc_i}{2}\right)\right]}{\sum \exp\left[-\left(\frac{\Delta AICc_i}{2}\right)\right]}$$

TABLE 3. *A priori* models considered to relate the effects of aquatic and terrestrial habitat parameters to *Triturus cristatus* and *T. marmoratus* larval abundance. (+) positive effects, (–) negative effects, EGG (= abundance of embryos) is included in all models. Intercept refers to the value on the Y axis where the line defined by the regression equation crosses the axis (if the complete absence of predictor variables has meaning, then the intercept represents that amount).

Model	Variables	Hypothesis	References
1	intercept only	Distribution not different from random	
2	EGG	No effects of ecological variables on larval abundance, EGG (+)	
3	OXY, SUVEG, FLVEG, LEAV, PRED, EGG	OXY (+) for embryo development, SUVEG, FLVEG, LEAV (+) as egg substrate, shelter, PRED (–)	Seymour & Bradford (1995), Wilbur (1997)
4	NIT*PHO, PRED, EGG	Reduced food level increases predation risk, NIT*PHO (+), PRED (–)	Anholt & Werner (1995), Thurnheer & Reyer (2001)
5	NIT*PHO, FLVEG, EGG	Higher productivity (+) and more floating vegetation (+) means more food	Braz & Joly (1994)
6	PH, OXY, EGG	Low pH (–) and oxygen (–) for embryo development	Seymour & Bradford (1995), Griffiths & de Wijer (1994)
7	PH, OXY, PRED, EGG	Low pH (–) and high oxygen (–) for predation risk	Kutka (1994), McIntyre & McCollum (2000)
8	DEPTH, SIZE, EGG	Pond size (–) for larval development	Pearman (1993; 1995)
9	DEPTH, SIZE, PRED, EGG	Greater incidence of predators with increased pond size (–)	Pearman (1993)
10	SHADE, EGG	Canopy cover (–)	Skelly *et al.* (1999; 2002)
11	SHADE, NIT*PHO, EGG	Canopy cover (–), productivity (+)	Skelly *et al.* (1999), Werner & Glennemeier (1999), Thurnheer & Reyer (2001)

Please note that there is an error in the equation describing AICc. The correct formula is AICc = -2 log-likelihood + 2K + ((2K(K+1))/(n-K-1)).
This is an error of presentation that does not affect the results.

TABLE 4. Ranking of *a priori* models relating embryo abundance of *Triturus cristatus* and *T. marmoratus* to aquatic and terrestrial habitat parameters. Ranking is based on smallest AIC_c value; $\ln\mathcal{L}$ = log likelihood, K = number of parameters in the model, w_i = Akaike's weight.

Model	$\ln\mathcal{L}$	K	AIC_c	ΔAIC_c	w_i
9	-27.82	5	67.939	0.000	0.733
8	-27.32	6	70.008	2.069	0.261
10	-34.04	4	77.556	9.617	0.006
6	-38.10	3	83.067	15.128	0.000
7	-37.78	5	87.874	19.935	0.000
4	-39.59	4	88.671	20.732	0.000
1	-41.67	2	91.875	23.936	0.000
3	-43.73	3	92.631	24.692	0.000
5	-42.89	4	94.044	26.105	0.000
2	-42.28	3	94.227	26.288	0.000

TABLE 5. Ranking of *a priori* models relating larval abundance of *Triturus cristatus* and *T. marmoratus* to aquatic habitat parameters. Ranking is based on lowest AIC_c value; $\ln\mathcal{L}$ = log likelihood, K = number of parameters in the model; w_i = Akaike weight.

Model	$\ln\mathcal{L}$	K	AIC_c	ΔAIC_c	w_i
11	40.55	5	-68.789	0.000	0.516
4	40.31	6	-68.307	0.482	0.406
5	38.63	6	-64.956	3.833	0.076
3	39.60	8	-56.941	11.847	0.001
10	31.05	4	-52.628	16.160	0.000
6	31.86	5	-51.413	17.375	0.000
2	28.81	3	-50.767	18.021	0.000
7	32.81	6	-50.253	18.536	0.000
8	30.29	5	-48.276	20.513	0.000
9	30.52	6	-45.681	23.108	0.000
1	13.03	2	-21.640	47.149	0.000

Akaike weights are data-dependent, posterior model probabilities (Burnham & Anderson, 1998). They can be used to calculate evidence ratios w_i/w_j that can be used to judge how much better a model is (a ratio of 3/1 would suggest that one model is three times better supported by the data than the other model; Burnham & Anderson, 1998).

We used regression procedure GENMOD in SAS (SAS Institute, 2001) to fit the models to the data and to obtain the log-likelihoods of the models that were needed for the calculation of AIC_c. The abundance of eggs was a variable with four classes. We therefore assumed a multinomial distribution and used the 'cumlogit' link function for modelling. For the abundance of larvae, we assumed a normal distribution and therefore used the 'identity' link function for modelling.

RESULTS

Eggs were observed in all ponds. Larvae were observed in 23 (72%) out of the 32 study ponds. In all ponds where embryo abundance was classified as very high, larvae were caught in 16% to 100% of the dipnet sweeps. Larvae were not observed in nine ponds categorised low to high in embryo abundance.

Model 9, representing the abundance of floating vegetation, pond size, and shade is the model that best explains variation in the abundance of embryos (i.e. lowest AIC_c value, highest Akaike weight; Table 4). This model explained 59.9% of the total variance. The highest abundance of embryos occurred in ponds intermediate in floating vegetation and shade (Fig. 1). Pond size was negatively correlated to embryo abundance (ß=-0.005, SE=0.002). Model 8, including the additional variable presence of hedgerows, ranked second, but was about three times less plausible (the ratio of the Akaike weights was 0.733/0.261). Model 10, including the variables best explaining the abundance of the larvae, was ranked third, but had less than 1% of the plausibility of Model 9. All other models had little or no support from the data. Thus, the abundance of embryos

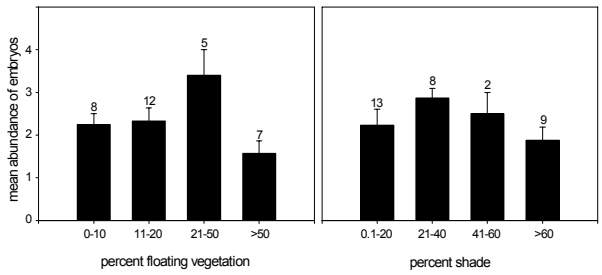

FIG. 1. Mean abundance of *Triturus cristatus* and *T. marmoratus* embryos (1 = low, 2 = moderate, 3 = high, 4 = very high) in response to extent of floating vegetation and extent of shade; error bars show S.E.; numbers above bars show sample size.

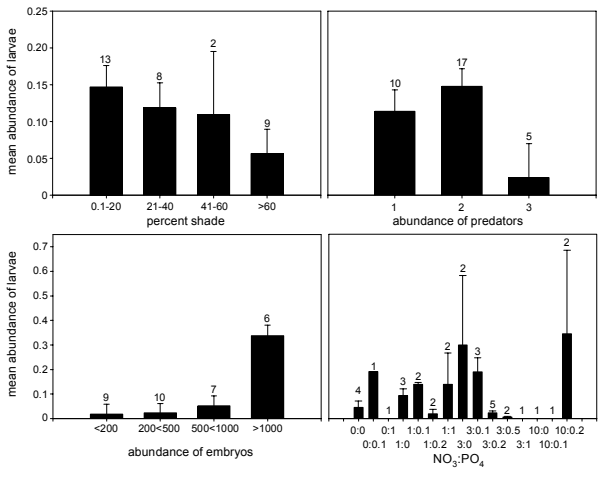

FIG. 2. Response of the abundance of *T. cristatus* and *T. marmoratus* larvae (measured in larvae per dipnet sweep) to extent of shade, abundance of predators, (1 = low, 2 = moderate, 3 = high), abundance of embryos and $NO_3 \times PO_4$ interaction; error bars show S.E.; numbers above bars show sample size.

was best explained by characteristics of the pond rather than the surrounding landscape.

The models suggest that environmental factors were important in regulating larval abundance. The abundance of embryos explained a large fraction of the variance in larval abundance (R^2=0.62), but the corresponding model (no. 2) was ranked only seventh (Table 5). The best model for larval abundance was model 11, containing shade and $NO_3 \times PO_4$, with shade being negatively – and abundance of embryos being positively – correlated with larval abundance (Fig. 2). Model 11 explained 82.1% of the total variance. It was followed by Model 4 which was 21% less plausible and included the variable predators instead of shade. The highest larval abundance was observed in ponds with moderate predator abundance (Fig. 2). All other candidate models did not exceed 1% of the maximum (Table 5).

DISCUSSION

The model selection analysis indicates that the abundance of eggs and larvae of the newts *Triturus cristatus* and *T. marmoratus* is influenced by environmental factors at the scale of the pond rather than at the scale of the surrounding landscape.

METHODOLOGY

The results must be viewed under the limitations of the semiquantitative data collection procedure of the abundance data (i.e. indices of abundance rather than estimates of abundance; Nichols, 1992; Anderson, 2001), particularly with regard to comparing ponds of different shapes and sizes. Temporal fluctuations in water parameters (NO_3, PO_4, pH, and oxygen), and changes ponds may have undergone during the study period remained undetected. A pond's size and maximum depth might be an insufficient approximation for hydroperiod. Embryos and larvae may have been over-proportionately spread in relation to pond perimeter in large ponds and hence more difficult to find, and the standardized dip netting might have been less efficient, for example, in more overgrown ponds than in ponds that were lacking underwater structures. However, dip netting does allow a large number of sites to be compared within a reasonable amount of time, and the catchability is equal across species (Arntzen, 2002) and we must assume that capture probabilities did not vary strongly across ponds. Eggs can be quantified more efficiently than adults which are more difficult to detect (Griffiths *et al*., 1996). However, different numbers of eggs laid by the two study species can bias the reflection of the adult population size (Arntzen & Hedlund, 1990). Another important aspect to be considered in the current study is the pooling of larvae from species that differ in landscape preference (Schoorl & Zuiderwijk, 1981). Previous studies failed to demonstrate clear ecological differences in and around syntopic ponds, and suggest that ecological niche segregation acts at the between-pond rather than at the within-pond scale (Jehle & Arntzen, 2000; Jehle *et al*., 2000). Moreover, the advantage of pooling two species with similar but not identical morphology and ecology lies in a more generalised signal in the data analysis. Finally, the binomial terrestrial variables might have been less suitable to detect potential effects than the more accurately measured aquatic parameters, as for example multinomial variables can not always be sufficiently quantified by binomial predictors.

Model selection based on information-theoretic methods offers a strong alternative to the more traditional null hypothesis testing approach and is simpler to implement than Bayesian methods (Johnson, 1999; Anderson *et al*., 2000; Olden & Jackson, 2000). Rather than asking whether the effect of an environmental factor is exactly zero (which is unlikely anyway), model selection methods ask which factors are necessary to adequately describe the data without over-parameterizing the statistical model (Burnham & Anderson, 1998). Analyses of similar data sets using multiple stepwise regression methods risk uncovering spurious patterns. In contrast, the candidate models were formulated before the analysis and are therefore not affected by random patterns in the data set (Burnham & Anderson, 1998; Anderson *et al*., 2001). Given that the ecology of amphibians in general and *Triturus* newts in particular is rather well understood (Griffiths, 1996; Wilbur, 1997), it seems preferable to use the existing knowledge to build candidate models. These models represent alternative biological hypotheses, to assess which one(s) of the hypotheses is or are best supported by the data, and to compare the relative support of alternative hypotheses, including those which are not nested (in a statistical sense; Burnham & Anderson, 1998; Anderson *et al*., 2001). Not all recorded variables listed in Table 1 were included in the analysis but served to extract the candidate models. We have studied only a small number of ponds and we therefore decided to use only simple candidate models (i.e. no interactions, except $NO_3 \times PO_4$, no quadratic terms, etc.). The distribution and abundance of newts is likely to be determined by a more complex interplay of ecological factors than we used in the candidate models; nevertheless, our best model was at least three times better than the other models. An analysis that attempts to uncover complex interactions between environmental factors and the distribution and abundance of newt larvae would probably have to be restricted to presence/absence data (see MacKenzie *et al*. (2002) for relevant methodology).

ABUNDANCE OF EMBRYOS

Surprisingly, embryo abundance was not related to terrestrial variables because embryo abundance is expected to reflect adult population size, which is most likely to be influenced by the terrestrial environment. The abundance of embryos was best explained by a combination of the amount of floating vegetation, pond size, and shading (canopy cover). The extent of aquatic vegetation has been shown previously to be a good indi-

cator for predicting site occupancy and abundance of newts (Cooke & Frazer, 1976; Oldham *et al*., 2000; Joly *et al.*, 2001), and is in accordance with our assumption that embryo abundance largely reflects adult population size. Aquatic vegetation provides a food source for prey organisms, cover from predators, and a substrate for egg laying. *Glyceria fluitans* was particularly important as an egg substrate, as already shown by other studies (Vallée, 1959; Miaud, 1995). However, beyond a certain plant density indicating an advanced stage of succession, ponds become unsuitable for newts as aquatic space gets restricted and drying probability increases (Oldham *et al*., 2000). The negative relationship of embryo abundance and pond size in the model opposes our hypothesis that large habitat patches may support large populations (e.g. Flather & Bevers, 2002), but agrees with Joly *et al*. (2001), who detected a negative relationship between pond area and abundance of newts. Pond area has also been shown to adversely affect survival, growth rate, and mass at metamorphosis of anuran tadpoles (Pearman, 1993).

Closed canopy cover has been shown to be negatively associated with the occurrence and performance of larval amphibians (Skelly *et al.*, 1999; 2002). An increase in aquatic and marginal terrestrial vegetation indicates an advanced stage of succession (Werner & Glennemeier, 1999), and as both study species are long-lived (Francillon-Vieillot *et al*., 1990), high embryo abundance might be the result of high recruitment in the past. Radio-telemetry has shown that more than 50% of adult *T. cristatus* and *T. marmoratus* utilized refuges within 15 m of a pond (Jehle, 2000), and the high embryo abundance might be caused by habitat preferences of the adults for areas with canopy cover. Indeed, more distant habitat features known to be important (hedgerows and woodland; Jehle, 2000; Jehle & Arntzen, 2000; Joly *et al*., 2001) were not included in the best model. The terrestrial buffer width necessarily incorporates a gradual decline in relative use with distance from the pond, making a clear delineation difficult. Moreover, the binomial terrestrial parameters probably were less powerful to assess their impact on embryo abundance than the measured aquatic parameters.

Abundance of Larvae

Two models for larval abundance were almost equally well supported by the data (evidence ration w11/w4 = 1.27). Both models included productivity (the nitrogen-by-phosphorus interaction) and embryo abundance. They differed in the other variables, which was shade in the best model and predator abundance in the second-best model.

Productivity of breeding sites has been shown to affect the survival of anuran larvae (Thurnheer & Reyer, 2001). Canopy cover and shading of breeding ponds negatively affect productivity and hence are important parameters for larval performance (Werner & Glennemeier, 1999; Skelly *et al.*, 1999; 2002). Open canopy ponds often exhibit supersaturated oxygen levels after midday, whereas no diel increase in dissolved oxygen can be observed in closed canopy ponds (Werner & Glennemeier, 1999; personal observations). Differences in oxygen concentrations also indicate differences in primary production for which both nitrogen and phosphorus are key nutrients. High concentrations of nitrates resulting from agricultural fertiliszer run off and urban drainage can have lethal effects on amphibian larvae (Hecnar, 1995; Watt & Jarvis, 1997). However, the positive correlation of NO_3 and PO_4 with larval abundance implies that prime nutrients tend to become limiting factors in the extensively used landscape of the study area. Closed canopy ponds also usually contain few macrophytes and small plankton populations, reducing food availability (Braz & Joly, 1994; Werner & Glennemeier, 1999). Predator presence was included in the second best explanatory model. Abundance of predators and amphibian larvae have been shown to correlate positively as both are likely to be related in a similar way to pond productivity (Thurnheer & Reyer, 2000). In contrast to other newt species, larvae of *T. cristatus* show no plasticity in morphology and an increase in activity in the presence of predators and should hence be more vulnerable to predators than other species (Schmidt & Van Buskirk, 2001). This might explain the low abundance of newt larvae in predator rich ponds. The lowest predator abundances occur in small, non-permanent ponds, which however are also associated with high risks of pond desiccation prior to metamorphosis (Griffiths, 1997; Pearman, 1995).

CONCLUSION

The abundance of embryonic and larval *Triturus* newts can be well described using parameters of the aquatic habitats. An important feature for both embryos and larvae was shading, suggesting that the successional stage of the pond or its surroundings are important. If the successional stage determines the abundance and possibly performance of premetamorphic newts, then this is likely to also affect population persistence (Skelly *et al*., 1999; 2002). This in turn suggests that under natural conditions population persistence and local extinction are influenced by deterministic factors and stochastic factors play a minor role (Skelly & Meir, 1997). However, in cultivated landscapes, stochastic events due to human activities (e.g. ditching, filling in) may still have severe impact on amphibian populations on a longer timescale.

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